

# A COMPARISON OF BIRD COMMUNITY STRUCTURE AND DIVERSITY ACROSS FOUR TROPICAL LIFE ZONES

KATHERINE W. MANARAS, EMILY M. MAHAR, JAMES A. MACINTOSH, CHERYL B. SHANNON, JESSICA S. VEYSEY, AND LAURA P. NAGY

*Abstract:* Variation in the diversity of bird communities of tropical life zones may be explained by differences in habitat structural complexity, as defined by niche diversity and food availability. This study examined the morphological diversity and community composition of four Costa Rican forest types that vary in structural complexity. As predicted, species diversity and morphological variance within foraging guilds were greatest in the lowland tropical rainforest, followed by submontane tropical cloud forest, and finally tropical dry forest.

*Key Words: diversity, guild, morphology, niche differentiation*

## INTRODUCTION

It is well known that tropical bird communities are more diverse than temperate bird communities. However, diversity is not uniform within the tropics and varies over a range of forest types (Stiles 1993). Kim et al. (1999) found that avian diversity was highest in tropical lowland forests, lowest in tropical dry forest and intermediate in montane cloud forest. One hypothesis that explains these differences suggests that increased habitat or structural diversity allow for greater niche differentiation, and hence facilitate greater species diversity. If so, greater niche differentiation in structurally complex forests should result in greater variance in avian morphology.

While Kim et al. relied upon auditory counts to describe the overall avian diversity of these forests, our project employed more intensive localized sampling with nets, which allowed us to collect morphological measurements of birds in the understory community. Because wet lowland forests contain more microhabitats and provide a greater diversity of available food resources than dry and montane forests (Stiles and Skutch 1989), we predicted higher species diversity and greater morphological variation in wet lowland forests.

## METHODS

We censused the understory bird community of four tropical forests in Costa Rica: Palo Verde National Park (lowland tropical dry forest), Monteverde Cloud Forest Preserve (mid-elevation montane forest), Corcovado National Park (lowland tropical rain forest) and La Selva Biological Station (lowland tropical rain forest). Based on information from Stiles (1993) on the diversity of microhabitats and food availability in these forests, we ranked them in ascending order of structural complexity as follows: Palo Verde, Monteverde, Corcovado, La Selva.

Ten nets were placed along accessible trails in secondary forest at each site for one day (12 January, 21 January, 3 February and 14 February 2000, respectively), and were open between 06:00 and 11:00. We recorded species, bill length, bill width, bill height, tarsus length, wing length, wing width and mass of all birds caught. To compare species diversity, productivity and foraging guild composition for each forest, we calculated the Shannon-Weiner diversity index, number of individuals caught, and the number of species per foraging guild. To compare variation in morphological traits across forest types, we used a principle components analysis to reduce the morphological measurements into two synthetic variables (1st and 2nd axes). For species represented by more than one individual, we calculated an average for each variable so that each species was represented by only a single data record. *Site Descriptions* (Hartshorn 1983): Palo Verde is a pacific slope lowland tropical dry forest that receives 1 - 1.5 m annual rainfall and is highly seasonal, with a 6 month dry season. Monteverde is a mid-elevation (1500 – 1800 m) montane cloud forest with 2 - 3 m of annual rainfall and little seasonal change. Corcovado, a southern lowland tropical rain forest has high annual rainfall (3 – 6 m) and a experiences a 3 month dry period. La Selva is a northern lowland tropical rain forest with 3 – 4 m of annual rainfall and little seasonal change.

## Results

Species diversity, as described by the Shannon-Weiner Diversity Index, was highest at La Selva, followed by Corcovado, Monteverde, and Palo Verde (H ± SE = 2.83 ± 0.047, 2.51 ± 0.046, 2.09 ± 0.073, and 2.02 ± 0.084, respectively; Table 1). Species richness was highest at La Selva, followed by Monteverde, Corcovado and Palo Verde. Species richness was two times higher at La Selva than at Palo Verde, but varied little between La Selva, Monteverde, and Corcovado (Fig. 1; Table 1). The number of individuals, which was the most variable of all measures, was highest at Monteverde, followed by La Selva, Corcovado and Palo Verde (Fig. 1; Table 1).

We observed wide variability in guild representations among sites (Fig. 2) Palo Verde was dominated by nectivores, had relatively few insectivores and no frugivores. Insectivores were the dominant guild at Monteverde and Corcovado. There were no granivores at Corcovado. No one guild dominated the bird community of La Selva, although insectivores and granivores were more common than the three other guilds caught at this site.

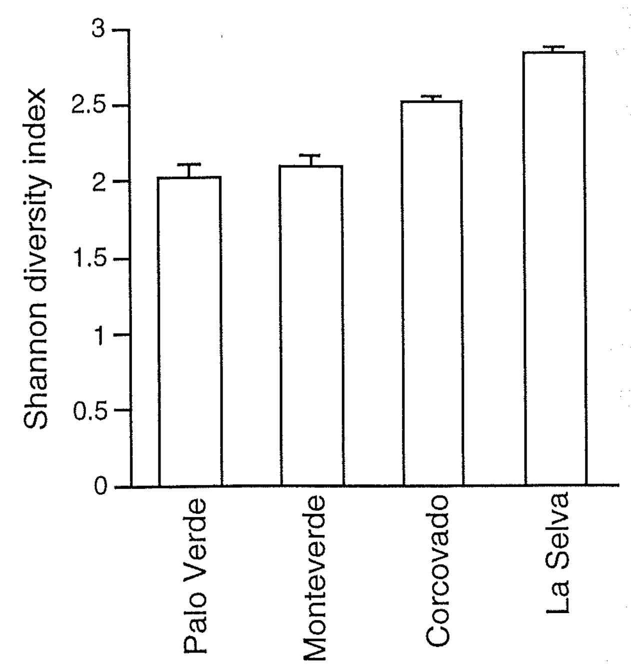


Figure 1. Shannon diversity index for understory bird diversity for 4 forest sites in Costa Rica.

The first principal component explained 63% of the variance in species morphological traits and was primarily determined by positive correlations between wing and bill length, wing width, and bird weight. We interpreted the first axis (PC – 1) as a measure of body size. The second principal component was most influenced by bill width and depth, and explained an additional 12.6 % of variability in morphology. We interpreted PC – 2 as a measure of bill shape (Table 2). Analysis of morphological differences of birds among sites based on PC – 1 and PC – 2 suggested that the widest range of body size and bill shape was found at La Selva. In contrast, although body size ranged widely at Corcovado, there was relatively little variation in bill shape. Both body size and bill shape were small and relatively invariant at Monteverde. Palo Verde only included two species.

Table 1. Rank order of species diversity, species richness, and number of individuals. Highest Ranks are at the top, lowest ranks are at the bottom of table.

| Rank | Diversity | Species Richness | # of Individuals |
|---|---|---|---|
| High | La Selva | La Selva | Monteverde |
| | Corcovado | Monteverde | La Selva |
| | Monteverde | Corcovado | Corcovado |
| Low | Palo Verde | Palo Verde | Palo Verde |





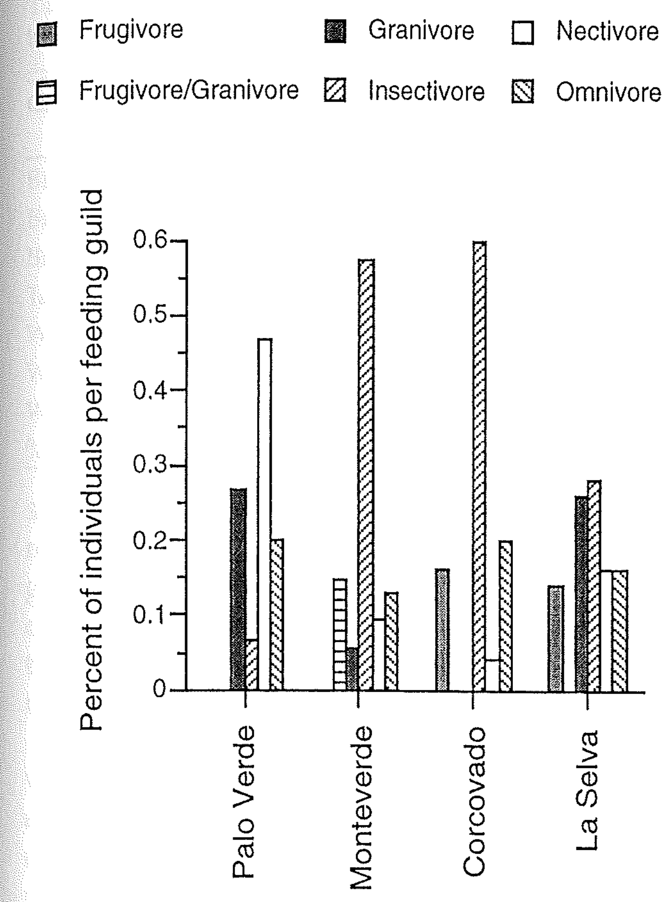


Figure 2. Relative proportion of individuals per feeding guild captured in the understory of each of four Costa Rican forests.

La Selva had the widest range of morphological variation within guilds. Morphological variation within guilds was relatively less variable at Corcovado, and quite invariant at Monteverde and Palo Verde. The range of morphological variation was especially large among the insectivores of La Selva. Insectivore bill shape was equally variable at Corcovado, but body sizes were smaller and more narrowly distributed (Fig. 3).

## Discussion

The avian diversity of understory forests increased with our rank of structural diversity and followed the same trend of overall avian diversity reported by Kim et al. (1999). However, species richness may be a better indicator of niche differentiation, suggesting that the less structurally complex Monteverde actually provides more niches than Corcovado. This apparent contradiction may be explained by the relative habitat uniformity at Corcovado, which contrasted with La Selva and Monteverde, where there were some open fields and/or agricultural land near our sampling sites. The birds inhabiting the additional niches provided by these fields may have contributed to the high species richness of La Selva and Monteverde. Similarly, the fields may increase the food availability for birds. The high captures at Monteverde were due to the disproportionately high abundance of one species, the Olive-sided Flycatcher, which is common in fields and clearings (Stiles and Skutch 1989) and composed 43% of all individuals caught.

Differences in structural and seasonal complexity may also explain the variation in foraging guild structure between the four forests. Highly seasonal rainfall results in distinct, pulses of flowers and fruits at Palo Verde. Our sampling coincided with the start of the dry season, a time when flowers are abundant and fruits are rare. This explains the high proportion of nectivores and the absence of frugivores at Palo Verde. Frugivores may become more abundant at Palo Verde as the dry season progresses and frugivorous altitudinal migrants arrive. High epiphyte load and high, relatively constant precipitation at Monteverde (Barnhorst et al. 1995), may provide a multitude of microhabitats suitable for insect breeding. The combination of both a diverse and abundant insect assemblage

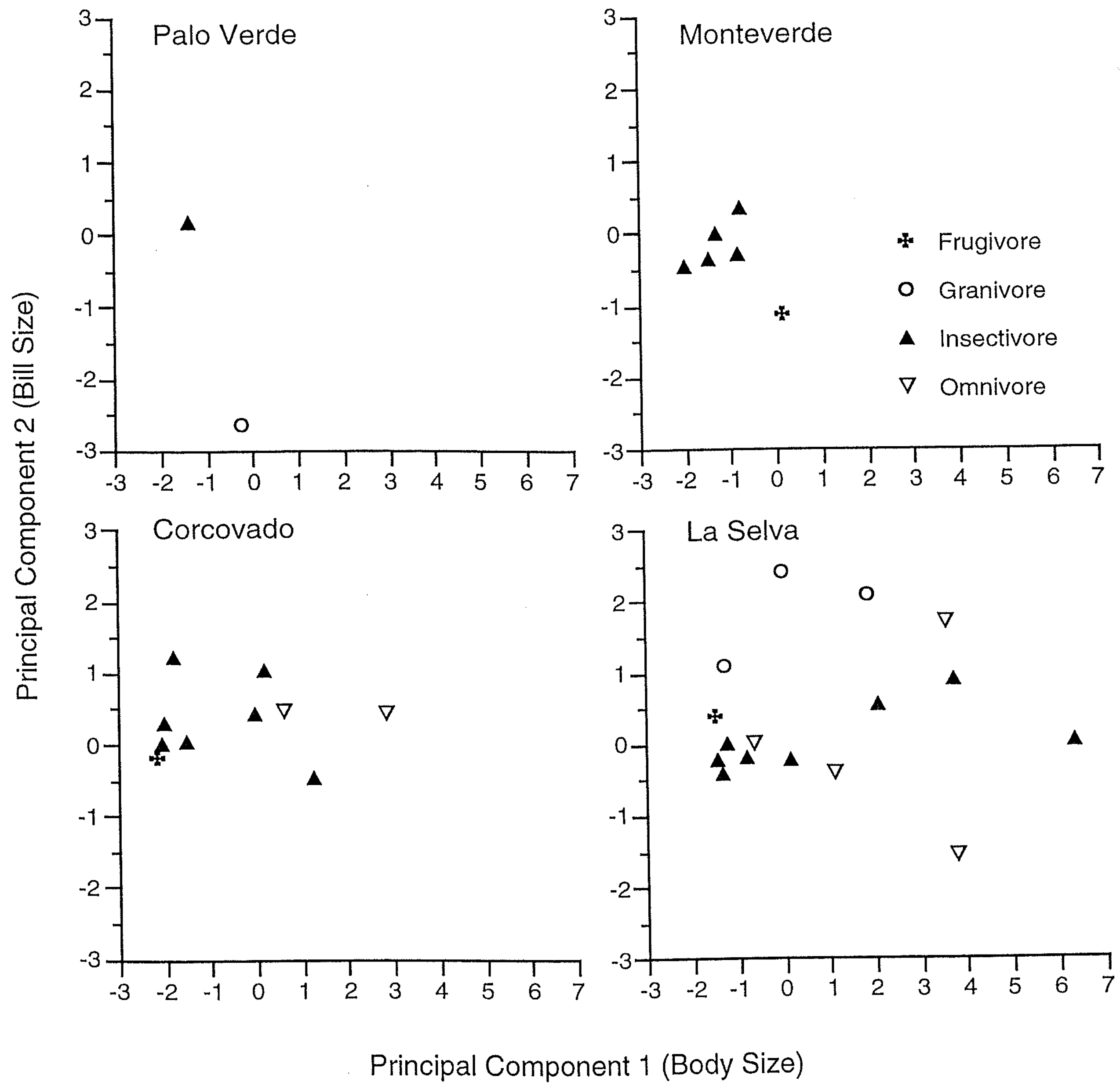


Figure 5. Relationship between body size and bill size (principal components 1 and 2) or morphological measurements of birds sampled in the understory of 4 Costa Rican forests. Feeding guilds are separated into 4 categories based on the dominant food type.

would explain the dominance of insectivores in this forest. Similarly, the prevalence of insectivores at Corcovado may be explained by the site's high mean annual rainfall, which produces many pools that support insects. The constant abiotic environment and high structural complexity at La Selva apparently provides a constant, wide range of food resources for all foraging guilds.

The wide range of insectivore body size at La Selva indicates that high morphological diversity is associated with high structural complexity of habitats. Morphological diversity within foraging guilds is the likely result of foraging specialization. A better comparison of variation in guild morphology between





Table 2. Principle component loading scores and % contributions of morphological measurements.

| Characteristic | PC #1 Loading Score | PC #2 Loading Score |
|---|---|---|
| Bill length | 0.41 | 0.04 |
| Bill width | 0.34 | 0.53 |
| Bill height | 0.35 | 0.5 |
| Tarsus length | 0.28 | 0.26 |
| Wing length | 0.42 | -0.37 |
| Wing width | 0.43 | -0.29 |
| Weight | 0.39 | -0.41 |
| % Contribution | 63.44 | 12.57 |

sites could be made if morphological measurements were available on more species per guild at each site. However, this may be difficult or impossible, as our results indicate that there are fewer species per guild at less structurally complex sites.

This study suggests that both seasonal variability and habitat structural complexity are important determinants of tropical forest avian communities. These factors affect the relative abundance of guilds and the morphological diversity within guilds through their effects on food type and abundance. A comparative investigation of avian food resources across these forests would allow us to more accurately describe diversity of guilds in relation to niche diversity.

## Literature Cited


Barnhorst, A. V., W. L. Osterling, N. E. Perlroth, N. D. Pouliot, and C. D. Wray. 1995. A comparison of forest structure at four locations in Costa Rica. Pp. 139-142 *in* C.D. Wray, and N. D. Pouliot, eds. Dartmouth Studies in Tropical Ecology 1995. Dartmouth College: Hanover, NH.

Hartshorn, G. S. 1983. Introduction to plants. Pp. 118-144 *in* D. H. Janzen, ed. Costa Rica Natural History. University of Chicago Press: Chicago, IL.

Kim, A. M., C. R. E. Dallison, B. J. Garcia, M. S. Kim, and M. A. Novello. 1999. Comparison of avian diversity, abundance and composition in four Costa Rican forests. Pp. 101-104 *in* D. R. Hogan and M. R. Babineau, eds. Dartmouth Studies in Tropical Ecology 1999. Dartmouth College: Hanover, NH.

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press: Ithaca, NY.

Stiles, F. G. 1993. Birds: Introduction. Pp. 502 – 530. *in* D. H. Janzen, ed. Costa Rica Natural History. University of Chicago Press: Chicago, IL.

Appendix 1. Understory avian community composition, arranged by site. Foraging guilds are C (carnivore), F (frugivore), G (granivore), I (Insectivore), N (nectivore), and O (omnivore).

| Site | Species | Guild | Abundance |
|---|---|---|---|
| Palo Verde | Common ground dove | G | 2 |
| | Ferruginous pygmy owl | C | 1 |
| | Hummingbird sp. | N | 7 |
| | Rose-Throated Becard | O | 1 |
| | Rufous-Capped Warbler | I | 1 |
| | Turquoise-Browed Motmot | O | 2 |
| | White-Tipped Dove | G | 2 |
| Monteverde | Black-faced solitare | F/G | 7 |
| | Chestnut capped brush finch | G | 1 |
| | Common bush tanager | O | 3 |
| | Golden-winged warbler | I | 1 |
| | Mountain elanea flycatcher | I | 1 |
| | Nightengale thrush | O | 3 |
| | Olive-striped flycatcher | I | 23 |
| | Purple-throated mountain gem | N | 3 |
| | Slaty antwren | I | 1 |
| | Slaty-based nightingale thrush | I | 2 |
| | Spotted barbtail | I | 1 |
| | Striped-tailed Hummingbird | N | 2 |
| | Swainsons thrush | F/G | 1 |
| | Three-striped warbler | I | 1 |
| | White-throated spade bill | I | 1 |
| | Yellowish flycatcher | I | 1 |
| | Yellow-throated brush finch | G | 2 |
| Corcovado | Black-throated trogon | O | 1 |
| | Blue-crowned manakin | F | 4 |
| | Eye-ringed flatbill | I | 1 |
| | Flycatcher sp. | I | 2 |
| | Golden-crowned spadebill | I | 2 |
| | Gray-headed tanager | O | 4 |
| | Long-tailed hermit | N | 1 |
| | Long-tailed woodcreeper | I | 2 |
| | Ochre-bellied flycatcher | I | 3 |
| | Plain ant vireo | I | 1 |
| | Ruddy-tailed flycatcher | I | 1 |
| | Russet antshrike | I | 1 |
| | Slaty antwren | I | 2 |
| La Selva | Band-tailed Barbthroat | N | 2 |
| | Barred woodcreeper | I | 1 |
| | Bay wren | I | 1 |





Appendix 1 cont. (La Selva)

| Species | Guild | Abundance |
|---|---|---|
| Blue-black grosbeak | G | 1 |
| Bright-rumped attila | I | 1 |
| Bronzy hermit | N | 1 |
| Buff-throated saltator | O | 2 |
| Clay-colored robin | O | 4 |
| Gray catbird | O | 1 |
| Green honeycreeper | O | 1 |
| Kentucky warbler | I | 1 |
| Little hermit | N | 1 |
| Ochre-bellied flycatcher | I | 2 |
| Red-footed plumeleteer | N | 2 |
| Rufous-tailed hummingbird | N | 2 |
| Thick-billed seedeater | G | 1 |
| Variable seedeater | G | 1 |
| Wedge-billed woodcreeper | I | 4 |
| White-breasted wood-wren | I | 2 |
| White-collared manakin | F | 7 |
| Yellow-billed cacique | I | 2 |